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Some Effects of Impoundment on the Environment and Growth of Brown Trout (*Salmo trutta* L.) in Loch Garry (Inverness-shire)

By R. N. CAMPBELL, B.Sc.

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By R. N. CAMPBELL, B.Sc.
Freshwater Fisheries Laboratory, Pitlochry

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Since the preparation of this paper Mr. Campbell has accepted an appointment with the Nature Conservancy, Hope Terrace, Edinburgh.

Some Effects of Impoundment on the Environment and Growth of Brown Trout (*Salmo trutta* L.) in Loch Garry (Inverness-shire)

INTRODUCTION

It is well known that trout feeding over newly-flooded land show a striking increase in size in a comparatively short time and that in many cases this improved rate of growth does not persist. There are few detailed accounts, however, of the effects of impoundment on a trout population in the British Isles and the observations made on trout in Haweswater (Frost, 1956) and in Loch Tummel (Campbell, 1957) dealt mainly with changes in growth rate. No direct data were recorded on changes in feeding habits or in the biological environment. There are some general references to the beneficial effects of impoundment on the growth of trout, e.g. for Loch Katrine (Fishery Board Reports for Scotland, 1889), Blagdon Reservoir (Carr, 1926), Ladybower Reservoir (Thompson, 1946), Eyebrook Reservoir (Oliver, 1948), Pollaphuca Reservoir (1948), while many other instances have resulted from the activities of the North of Scotland Hydro-Electric Board during the last twelve years. There are, however, several accounts of the effects of impoundment on the growth of trout and other fish and on their invertebrate food fauna from Scandinavia and North America (e.g. Runnström, 1951; Nursall, 1952; Aass, 1958), but little information exists on the food and feeding habits of trout during the initial stages of impoundment. Furthermore, water level conditions in Scottish reservoirs (including hydro-electric reservoirs), are not normally the same as those in countries subject to a continental type of climate, where the maximum water levels occur each year during the summer as the result of melting snow, while minimum levels are encountered during the winter months. In Scotland the reverse is generally the case.

The object of this study was to follow through the sequence of events in a newly-made hydro-electric reservoir that affect the food and feeding habits and, consequently, the growth of trout, as well as to observe the major changes in their environment that took place during this transitional period. This was to be accomplished by recording the food and growth of samples of trout caught at regular intervals over a successive period of years, commencing before impoundment. Loch Garry was considered suitable for this investigation as pre-flooding sampling was possible and a biological survey had recently been carried out (Hamilton, personal communication).

DESCRIPTION OF LOCH GARRY

Loch Garry occupies the eastern section of Glen Garry in Inverness-shire and lies along the course of the River Garry which flows from Loch Quoich, through Loch Garry and on into Loch Oich. Loch Oich discharges into Loch Ness at Fort Augustus by the River Oich.

In connection with hydro-electric developments in the area, the waters of Loch Garry were impounded by a dam erected near its eastern end which was completed in December 1955. The closure of the dam created a reservoir which is about seven miles long and has, at normal water level, a surface area of about 1,570 acres. The new impoundment is elongated, slightly curved and has a width of about half-a-mile. The closure of the dam, which caused a rise in level of about seventeen feet, did not alter the width substantially but caused the loch to extend westwards for about two miles. Before impoundment the surface area of Loch Garry was 1,088 acres, so some 480 acres have been added to its surface area (Fig. 1). The maximum depth of the loch is now around 230 feet.

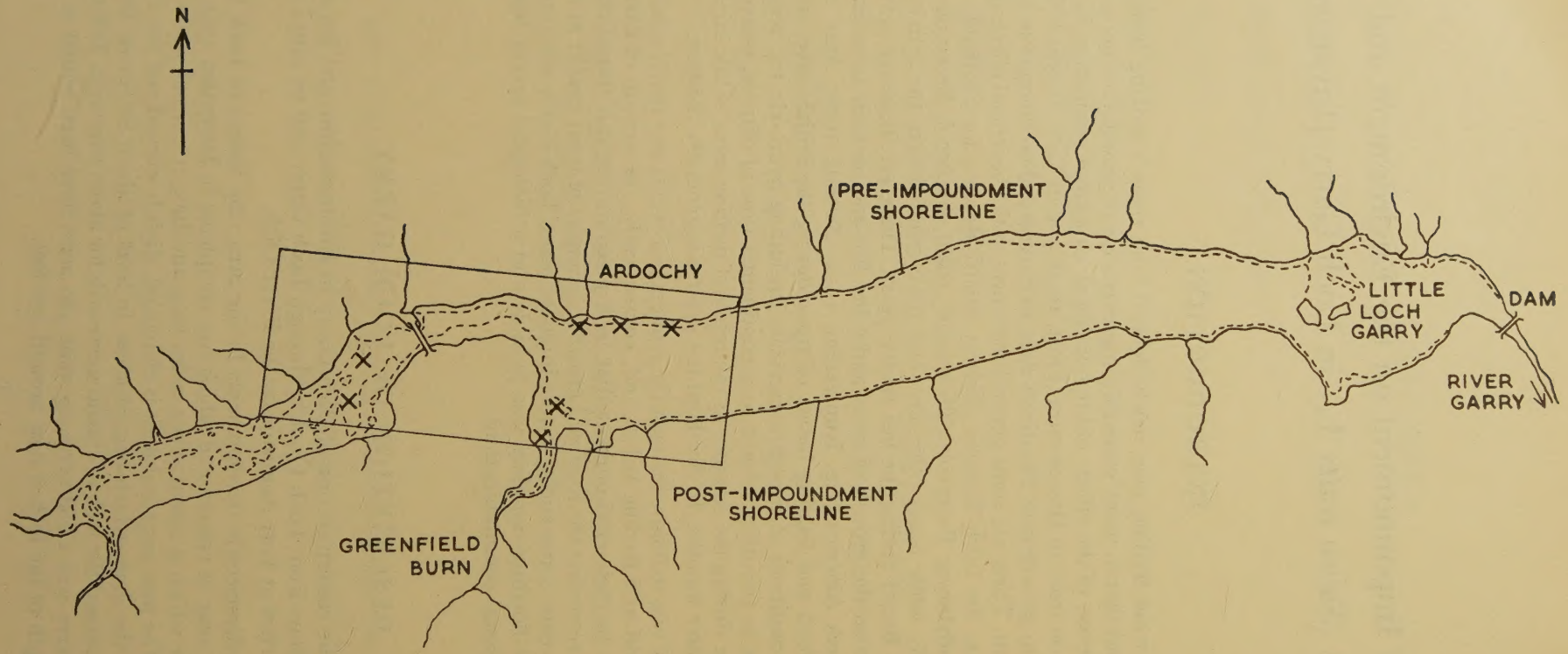


Fig. 1. Map of Loch Garry showing the shorelines before and after impoundment and the sampling sites (x). The boxed area indicates the extent of the aerial photograph in Plate 1.
(Scale: 2 ins. to 1 mile).

Most of the land flooded at the west end of the loch consisted of rough, marshy grazing with bog pools and occasional alder trees. The much smaller areas of land flooded along the steeper sides of the loch were mostly rough grazing with bracken, heather and some trees, mostly oak and birch, which were felled before flooding began. At the mouth of the Greenfield Burn, which entered the loch on the south side, an expanse of sand and shingle which formed an extensive delta was submerged (Plate 1). Before flooding, a small basin at the eastern end of the loch, known as 'Little Loch Garry' was separated from the main loch by an island and a promontory but, as a result of the rise in level following impoundment, this basin has lost its separate entity and the higher ground of the promontory now forms a second island.

The chemical characteristics of the water do not appear to have been affected by the rise in level. A post-impoundment pH value of 6·2 and total alkalinity of 3·0 parts per million (expressed as calcium carbonate) are within the range of pre-impoundment values (Hamilton, personal communication).

One of the characteristics of the loch before flooding was the large and rapid fluctuations of level that occurred, produced by the heavy rainfall to which the area is subject, and the narrow gorge through which the water from the loch was discharged at the eastern end. It seems likely that these natural fluctuations, together with a lowering of loch level during the early stages of the construction of the dam, resulted in a reduction in the numbers of the bottom fauna of the littoral zone (Hamilton, personal communication) and, as these fluctuations have continued since impoundment, they still have an effect on the food supply and feeding habits of trout in the loch (see Fig. 9).

In the past Loch Garry was regarded as a loch which contained a large population of small brown trout but which also produced some much larger trout, weighing up to twenty pounds (9·1 kg.). During the present investigation several large trout were recorded with weights ranging from 6 pounds (2·7 kg.) to 18 pounds (8·2 kg.). The present fish fauna of the loch consists of brown trout (*Salmo trutta* L.), char (*Salvelinus alpinus* L.), eels (*Anguilla anguilla* L.) and minnows (*Phoxinus phoxinus* L.), the last having been accidentally introduced since impoundment by anglers releasing unused live-bait. The new reservoir also continues to be accessible to salmon as a Borland lift was built into the dam. There are no records of sea trout (migratory trout) from Loch Garry.

The aquatic invertebrates usually associated with the main food of trout in lochs (Campbell, 1955, and others), e.g. planktonic Crustacea, Plecoptera, Ephemeroptera, Hemiptera, Trichoptera, Coleoptera, Diptera (Chironomidae), and Mollusca (*Sphaerium* spp., *Limnaea pereger*) are all represented in Loch Garry, with the exception of the benthic crustaceans, *Gammarus* and *Asellus*.

METHODS

Samples of trout were obtained during the angling season by rod and line and by baited ground lines. During the close season both angling and gill-netting were used but, in order to avoid catching salmon parr or smolts, no gill-nets were used with a smaller mesh than one inch (knot to knot) except in September 1959 and January and December 1960. Experience showed that most of the trout could be caught in nets with a mesh of one inch or one-and-a-quarter inches (knot to knot). Nets of these meshes were therefore used almost exclusively but occasionally a net of one-and-a-half inch mesh was set but scarcely any trout were caught in it. In consideration of the angling proprietors of the loch, efforts were made to limit the number of trout in each sample. When samples were collected by angling the numbers of trout caught could be easily regulated, but when nets were used these had to be inspected at intervals during the night and lifted when it appeared that a reasonable sample had been collected. During the six years (1955 to 1960 inclusive) a total of 839 trout was caught, an average of about 140 each year. These numbers do not include trout or details of trout (e.g. scales and stomach contents) that were supplied by the proprietors and other anglers. One of the proprietors of Loch Garry provided stomach contents from fish caught during the angling season and these samples supplemented the information obtained from the monthly samples. Grateful acknowledgement is made for this valuable help.

The length of each trout caught was measured (to the nearest millimetre) from the tip of the snout to the middle of the tail, a sample of scales was removed and the stomach contents were preserved for subsequent examination.

The first samples of trout from Loch Garry and the section of the River Garry which was to be flooded were collected, by angling, in May and September 1955. After impoundment had begun in December 1955 sampling was carried out each month until December 1958, when regular sampling was discontinued. Supplementary samples were, however, taken in May and September 1959 and in January and December 1960. The sample taken in May 1959 was collected primarily for a study of the stomach contents of the fish caught, while the other samples were collected for stomach contents and also to provide data on the length increments of all age classes of trout during 1959 and 1960.

RESULTS

A. Post-Impoundment Growth of Trout

The great majority (88%) of the trout from the area of Loch Garry where samples were collected (see Fig. 1), pass one year or less in a nursery stream. This may be compared with 100% in Three Dubs Tarn (Frost and Smyly, 1952), 15% in Loch Tummel (Campbell, 1957) and 12% in Windermere (Allen, 1938).

The effect of impoundment on the rate of growth of trout is summarised in Table 1 and in Fig. 2.

TABLE 1

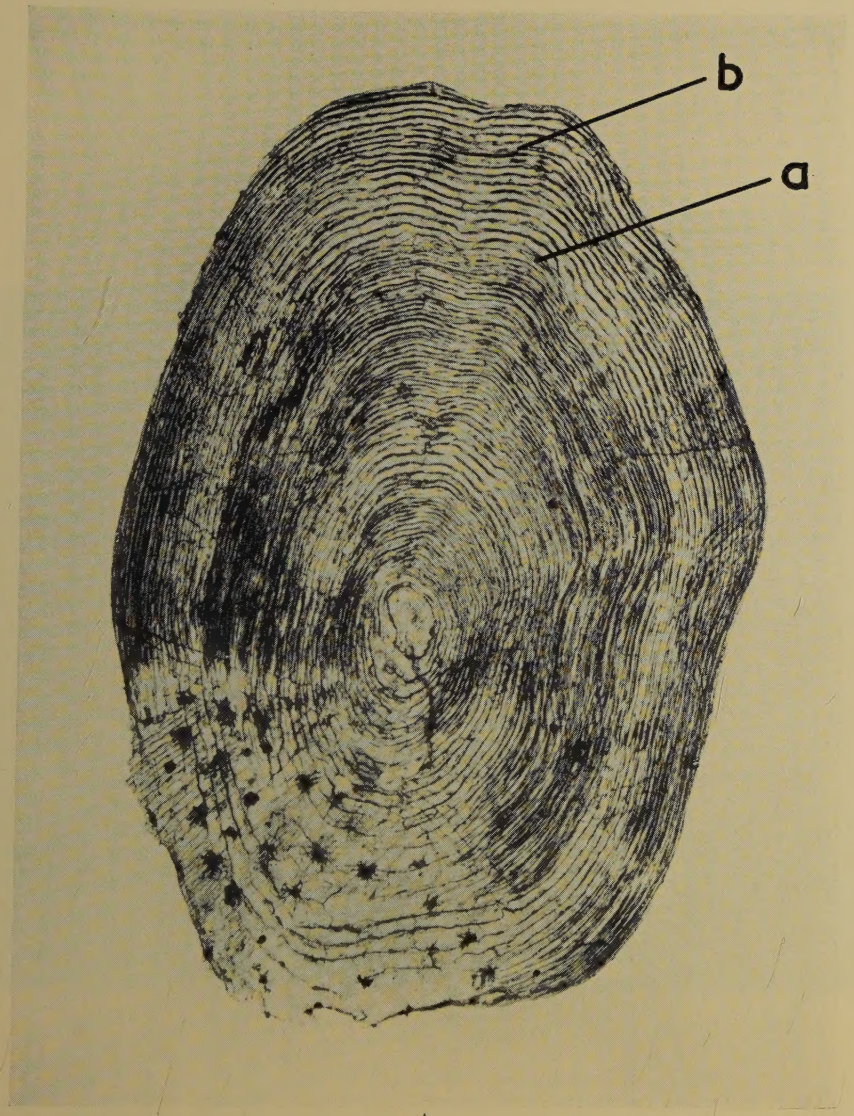
AVERAGE LENGTH FOR AGE OF TROUT BEFORE AND AFTER IMPOUNDMENT

Year Class	Length (cm.) at Age (yrs.): 1	2	3	4	5	6	No. of Trout
1949	6·5	13·7	18·1	21·7	23·8	26·7	10
1950	6·2	13·0	18·1	21·8	24·1	25·0	22
1951	7·6	13·5	18·1	21·8	24·0	**29·8**	88
1952	5·7	14·1	20·0	21·7	**27·1**	29·9	244
1953	6·3	13·8	18·3	**26·3**	29·5	32·5	408
1954	6·1	15·5	**22·3**	27·2	29·7	32·6	485
1955	5·0	**13·6**	21·1	26·0	32·5	—	560
Flooding							
1956	**5·5**	12·5	21·0	28·0	—	—	392
1957	7·1	16·5	22·6	28·1	—	—	268
1958	7·5	16·5	21·5	—	—	—	182
1959	7·5	15·6	—	—	—	—	74
1960	7·6	—	—	—	—	—	7

Trout that were in their third, fourth, fifth and sixth years when flooding took place showed a considerable increase in their rate of growth during 1956, the first year of impoundment. After 1956 this faster rate of growth was maintained by trout in their third year, while for trout in their fourth, fifth and sixth years the growth rate continued to increase further.

Trout in their first and second years did not show any immediate response to post-impoundment conditions in 1956, c.f. Loch Tummel (Campbell, 1957) and Haweswater (Frost, 1956), but during the following years an increase in the rate of growth of trout in both age-groups took place (see p. 18).

Plate 1. The western section of Loch Garry before impoundment (see Fig. 1). The post-impoundment shoreline is shown by the broken line and sampling sites are marked (x).



A

B

Plate 2. Scales from (A) immature and (B) maturing trout, autumn 1956. *a*, commencement of 1956 post-impoundment growth; *b*, summer check.

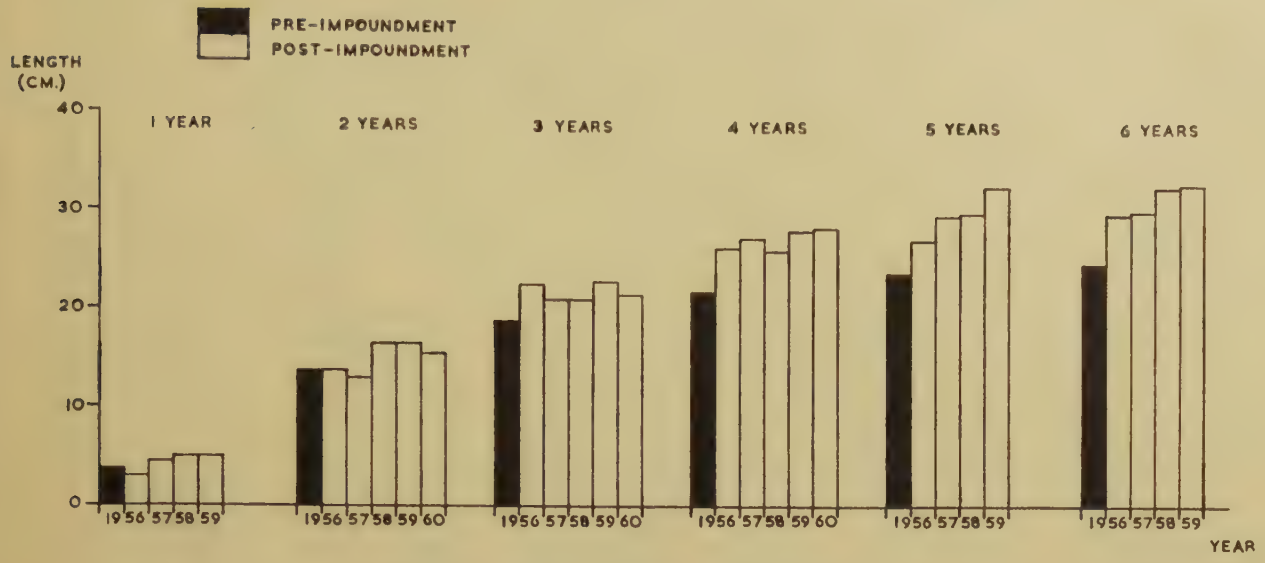


Fig. 2. Length for age of trout in Loch Garry

In Fig. 3 the effect of early post-impoundment conditions on the growth of trout in their third and later years is shown in terms of the estimated annual increment in weight. This figure was calculated by

Fig. 3. Estimated weight increment of trout in Loch Garry

plotting the logarithm of the average weight in grams at each centimetre of total length against the logarithm of the corresponding length in centimetres. Length and weight data were obtained from 79 trout sampled during the late summer, a time when the weight-length ratio is at its maximum value. In Fig. 4 the considerable increase in weight for age which took place, the yardstick of improvement

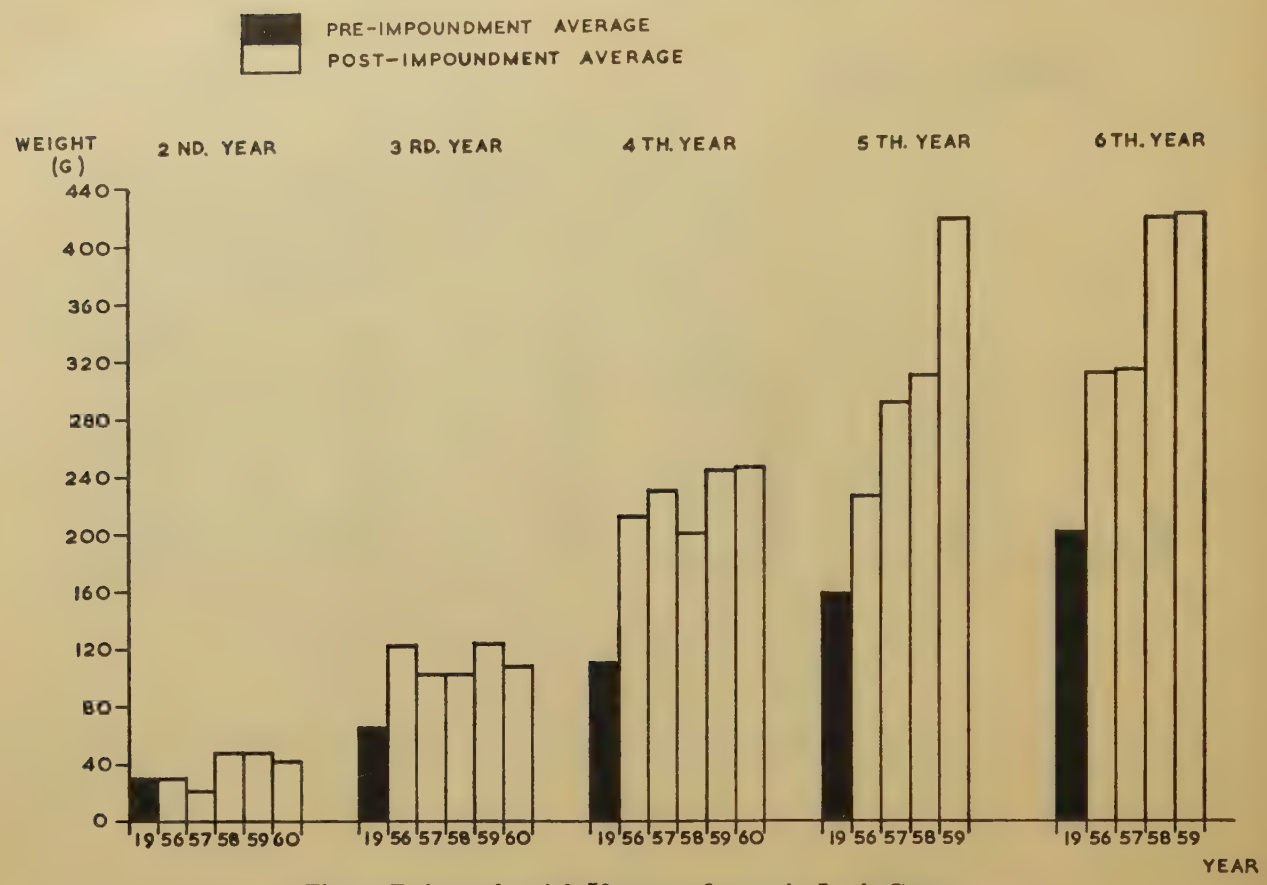


Fig. 4. Estimated weight for age of trout in Loch Garry

from the angler's point of view, is shown and the effect of impoundment on the angling status of the loch is shown in Table 2.

TABLE 2

PERCENTAGE WEIGHT COMPOSITION OF TROUT CAUGHT* IN LOCH GARRY

Year	No. of trout	Percentage			
		under 6 oz.	6-12 oz.	12-16 oz.	over 16 oz.
1955	40	90·0	7·5	2·5	—
1956	70	45·7	52·9	1·4	—
1957	95	17·9	58·7	22·4	1·0
1958	68	39·7	25·0	25·0	10·3
1959	136	51·5	38·2	9·6	0·7
1960	69	68·1	31·9	—	—

*All the trout were caught by angling, except in 1959 and 1960 when some were caught by angling (25 and 27 respectively) and some by netting (111 and 42 respectively). The mesh size of the nets used ($\frac{3}{4}$ to $1\frac{3}{4}$ in., knot to knot) sampled trout of the same size range as those caught by angling.

The minimum size of trout retained by anglers varies greatly with the locality but, considering all aspects, trout of 6 oz. (170 g.) would probably have been considered worth keeping by anglers fishing in Loch Garry. Thus, before impoundment, only about 10% of the trout were keepable. During 1956,

the first season after impoundment, the proportion rose to over 50% while in 1957 and 1958 the proportions were over 80% and 60% respectively, falling to just over 30% in 1960. The new rate of growth resulted in three age groups providing keepable trout of 6 oz. or over (four, five and six-year-old trout) whereas before impoundment fish of this size were mostly found in the five and six-year-old classes, or older, and consequently were few in number.

The first indication of a post-impoundment change in growth rate was contained in the sample of trout collected in mid-March 1956, when the scale margins of 29 out of the 54 trout (53%) sampled showed several widely-spaced rings, conventionally referred to as 'summer' growth, which signified the commencement of the current year's growth. Of the 72 trout previously sampled in January and February only 7 (10%) had scales which bore these widely-spaced rings, the extent of which was too small to measure. This figure may be compared with the observations of Ball and Jones (1960) on the trout in Llyn Tegid when the proportion of trout with this type of scale margin, sampled in January, was 11%.

In the March sample of 4+ years-old trout from Loch Garry, 12 showed an average growth increment of just over 1 cm. which represented about half the total annual increment in length that occurred before impoundment (Table 1). Similarly, of the 5+ years-old trout, 13 showed an average increment of 1 cm., which was again about half the total annual increment before impoundment. Four 3+ years-old trout also showed measurable increments. In the sample of trout collected in April 1956, some five weeks later, the scales of 25 out of the 29 trout (86%) sampled showed growth increments. There were only a small number of trout from each age group in this sample, but nine 4+ years-old trout showed an average of 1·6 cm. growth increment and eight 5+ years-old trout an average of 1·6 cm.

In the writer's experience, evidence of the current year's growth on scales of trout from Highland lochs is practically unknown as early in the year as March; the current growth increment is not usually measurable until May. For example, in a sample of 61 trout from Lochan-an-Daim (Perthshire) collected in the middle of April, only three (5%) showed a measurable growth increment on their scales. Similarly, in a sample of 837 trout from Kinnaird Mill Dam (Perthshire), collected between the end of April and early May, only 46% showed a growth increment and of the 84 trout of the 4+ and 5+ age groups only two (2·4%) showed any measurable growth increment.

These observations on the growth of trout in Loch Garry during the early months of 1956 show that relatively fast growth can be made by trout at low water temperatures (Table 3) and confirms laboratory experiments in which adult trout were found to grow throughout the winter when an abundance of food was available. A comparable field observation was made by Stewart (1955), who described a high, cold, Icelandic lake which produced good brown trout. The surface temperature in this lake in August of a warm summer was only 6·0°C.

TABLE 3

MEAN MONTHLY WATER TEMPERATURE (°C) AT LOCH GARRY DAM

Month	Year		
	1956	1957	1958
January	—*	3·7	2·0
February	—*	2·3	1·0
March	3·5	3·7	2·9
April	5·9	6·1	3·4
May	8·5	7·9	7·9
June	11·8	12·7	10·7
July	13·3	14·4	15·1
August	12·7	13·8	14·2
September	11·9	10·1	14·2
October	9·2	6·9	12·7
November	6·5	6·6	8·4
December	5·5	4·1	4·4

*During January and February 1956, the water temperature was only recorded on one occasion in each month. The readings were: January 30, 3·1°C; February 20, 2·9°C.

During 1956 the greatest relative increments in growth were made by immature trout of both sexes (Fig. 5). It is possible that the slower growth of maturing trout was due to the utilisation of food by the developing gonads, whereas in immature trout this could be used for body growth. The comparison of scales from these two classes of trout showed that 'summer' or fast growth took place in both during the spring or early summer. In July, the scales of maturing trout began to develop a 'winter' or slow

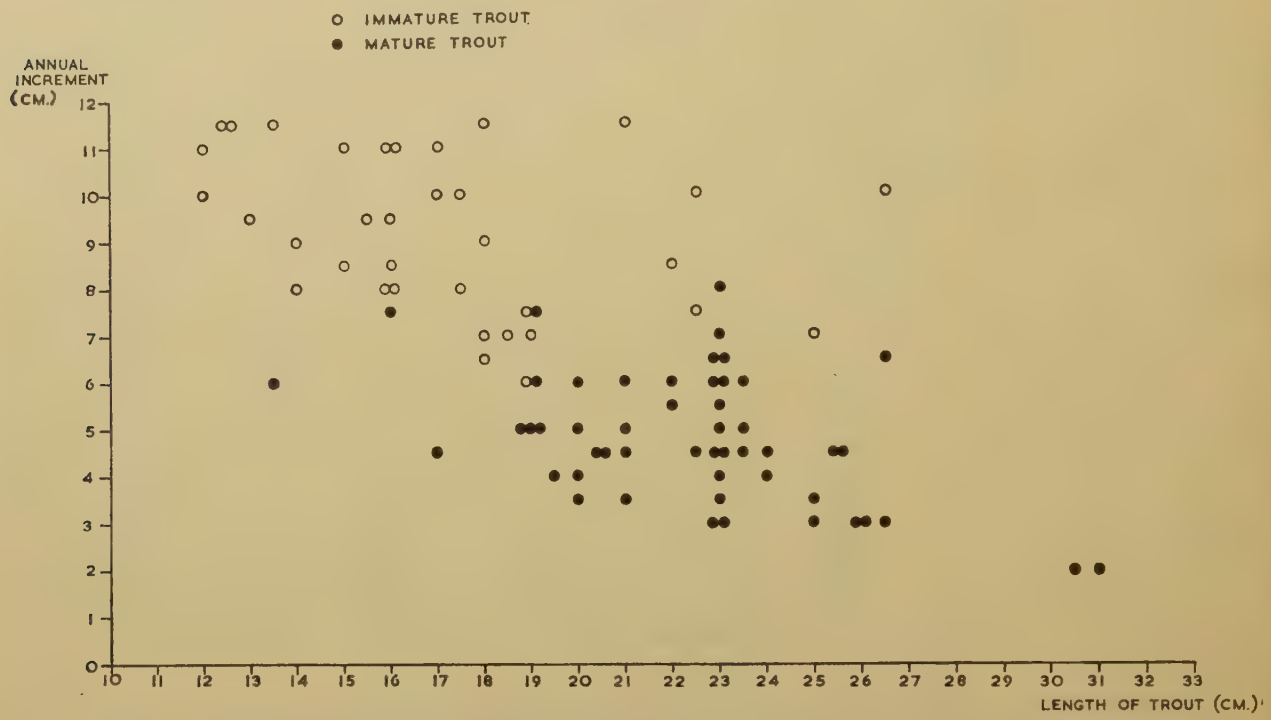


Fig. 5. Annual increments in length during 1956, from samples taken from November 1956 to March 1957 (inclusive).

growth zone, but the scales of immature trout, after showing a brief check in growth, continued to show 'summer' growth until the late autumn (Plate 2). This pattern of scale growth has been described by Ball and Jones (1960) for some trout in Llyn Tegid, but no reference is made to their degree of maturity.

B. Food and Feeding Habits

During the winter and spring of 1956 trout were sampled with gill-nets set during the hours of darkness so that no detailed picture of feeding habits was obtained. It was observed, however, that in March, when two nets were set over flooded heather moorland and three more were set over the grass and shingle of the Greenfield Burn delta, where earthworms had been observed, the first two nets did not catch any trout while the other three caught fifty-four, forty-two of which contained earthworms. It was also noticed that some trout were usually caught at the shore end of the gill-nets in less than one foot of water. These observations suggest that trout congregated over a newly-flooded area which contained earthworms, rather than over one that would not provide any, and that trout would forage for terrestrial organisms in shallow water as soon as these were made available by the rising water level. Runnström (1951) records that char collected over newly flooded bottoms and that their stomachs contained terrestrial insects and earthworms. The use of ground lines baited with earthworms during the winter of 1956 confirmed that trout moved into shallow water over newly flooded land at night in search of food as these lines were all set in water from less than one foot in depth to six feet, and only took trout during the hours of darkness.

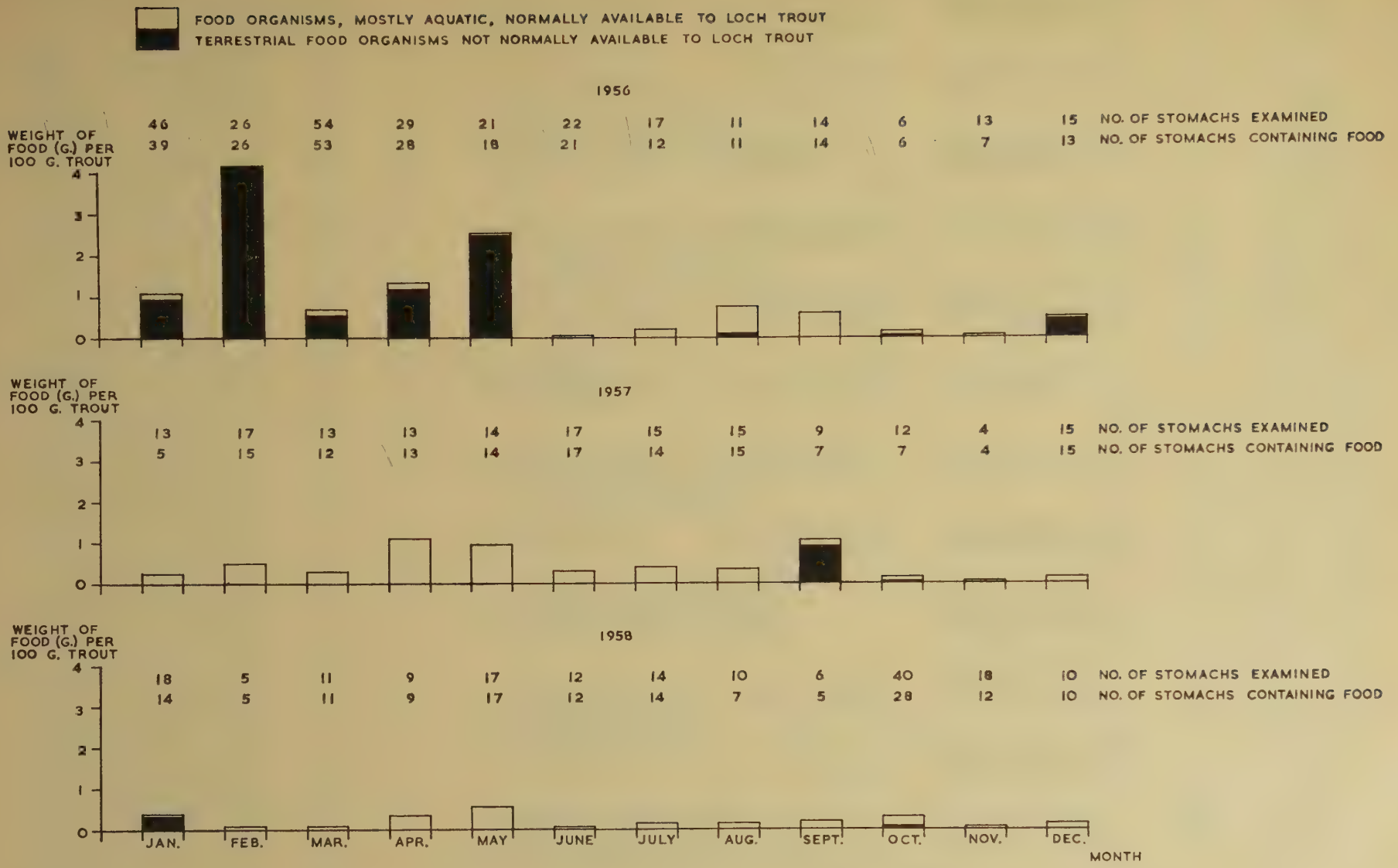

FOOD ORGANISMS, MOSTLY AQUATIC, NORMALLY AVAILABLE TO LOCH TROUT
TERRESTRIAL FOOD ORGANISMS NOT NORMALLY AVAILABLE TO LOCH TROUT
1956
WEIGHT OF FOOD (G.) PER 100 G. TROUT
46 26 54 29 21 22 17 11 14 6 13 15 NO. OF STOMACHS EXAMINED
39 26 53 28 18 21 12 11 14 6 7 13 NO. OF STOMACHS CONTAINING FOOD
0 1 2 3 4
1957
WEIGHT OF FOOD (G.) PER 100 G. TROUT
13 17 13 13 14 17 15 15 9 12 4 15 NO. OF STOMACHS EXAMINED
5 15 12 13 14 17 14 15 7 7 4 15 NO. OF STOMACHS CONTAINING FOOD
0 1 2 3 4
1958
WEIGHT OF FOOD (G.) PER 100 G. TROUT
18 5 11 9 17 12 14 10 6 40 18 10 NO. OF STOMACHS EXAMINED
14 5 11 9 17 12 14 7 5 28 12 10 NO. OF STOMACHS CONTAINING FOOD
0 1 2 3 4
JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
MONTH

Fig. 6. Loch Garry (weight composition of stomach contents)

The low water temperature (Table 3) did not appear to discourage trout from feeding. Figs. 6 and 7 summarise the food and feeding behaviour of trout in Loch Garry, based on monthly samples collected from January 1956 to December 1958, inclusive.

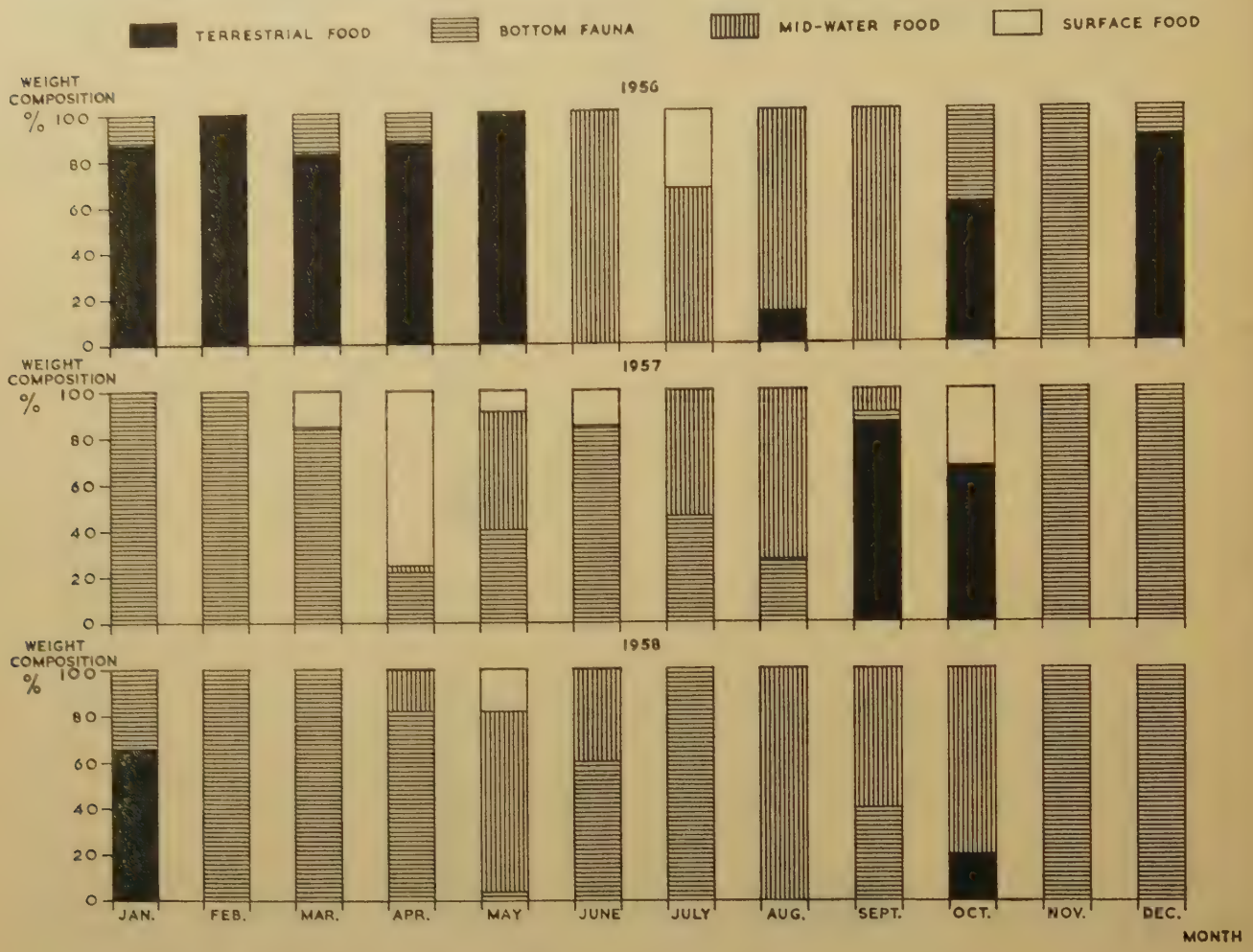


Fig. 7. Loch Garry (weight composition of stomach contents of trout)

In the first five samples after flooding (January to May, 1956) terrestrial food predominated in the stomach contents of the one hundred and sixty four trout which contained food. Only twelve were found to have empty stomachs.

In terms of weight the ratio of terrestrial organisms found in stomachs over this period to that of aquatic organisms was 19:1 and in numbers 4.3:1 so that, on the average, the weight of an individual terrestrial organism was between four and five times that of an aquatic organism. The most important terrestrial organisms were earthworms, providing five times the bulk of all the other terrestrial organisms together (Fig. 8). Table 4 shows the actual numbers of the various forms of terrestrial organisms found in trout stomachs during the first five months of flooding.

After earthworms, spiders (mostly lycosids) were the next most numerous organisms, but coleopteran, lepidopteran and dipteran larvae, though fewer in numbers, were of much greater bulk. The largest invertebrate terrestrial organisms found in trout stomachs, apart from the larger earthworms, were the

TABLE 4

FOOD OF TERRESTRIAL ORIGIN FOUND IN THE STOMACHS OF TROUT SAMPLED MONTHLY FROM JANUARY-MAY 1956 (INCLUSIVE)

Group	Total No. found
Annelida	
Oligochaeta	1380
Insecta	
Coleoptera, larvae	133
Lepidoptera, larvae	288
Diptera, larvae	150
Arachnida	
Araneida	683
Other organisms (chiefly adult Coleoptera)	45

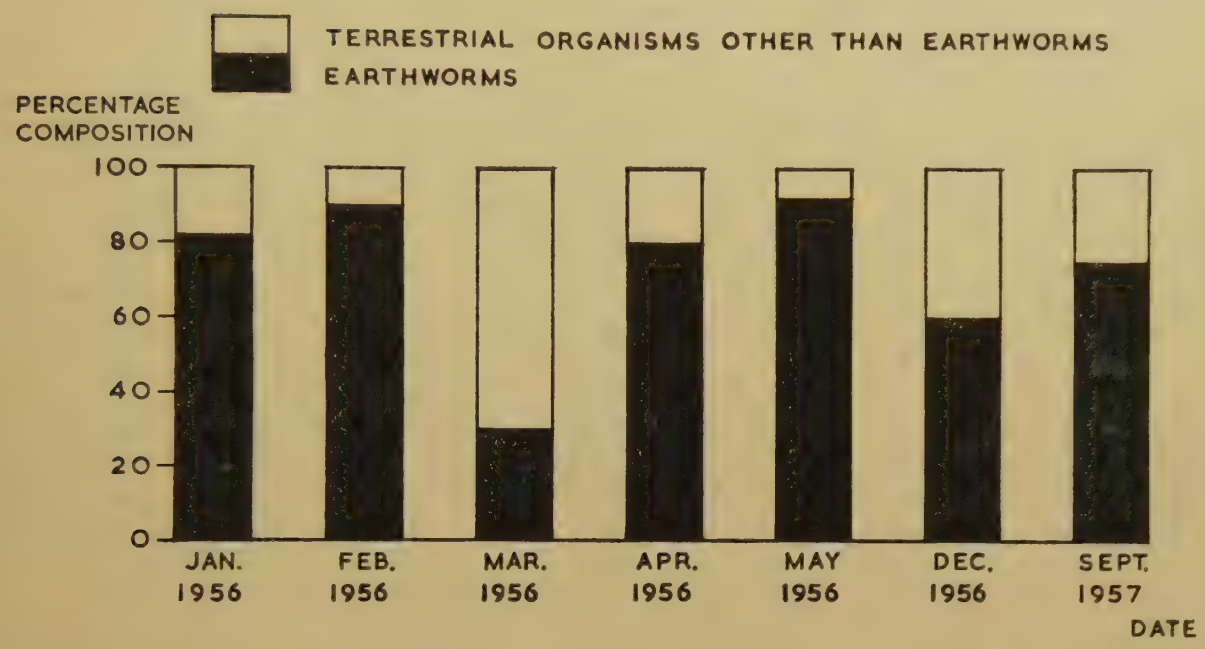


Fig. 8. Loch Garry, stomach contents of trout. The proportion of earthworms and other terrestrial organisms made available to trout by increases in loch level.

full-grown larvae of the fox moth (*Macrothylacia rubi*) which measure about 50 mm. in length and weigh about 2·25 g.

Adult Coleoptera found in stomachs during January and February 1956 were considered as being available to trout as a result of flooding but many of those found in stomachs from March onwards could have been available as surface food, together with other adult terrestrial and aquatic insects.

After May 1956 the appearance of terrestrial food in trout stomachs in substantial amounts was no longer a regular occurrence. This was not due to any change in the feeding behaviour of the trout as they were still being caught inshore, but probably because the dates of sampling did not coincide with periods when land which had not been previously submerged was flooded. The presence of terrestrial organisms in the stomachs of trout sampled in August, October and December 1956 (Fig. 6) can be correlated with progressive increases in loch level (Fig. 9). Terrestrial organisms were also found in the stomachs of trout

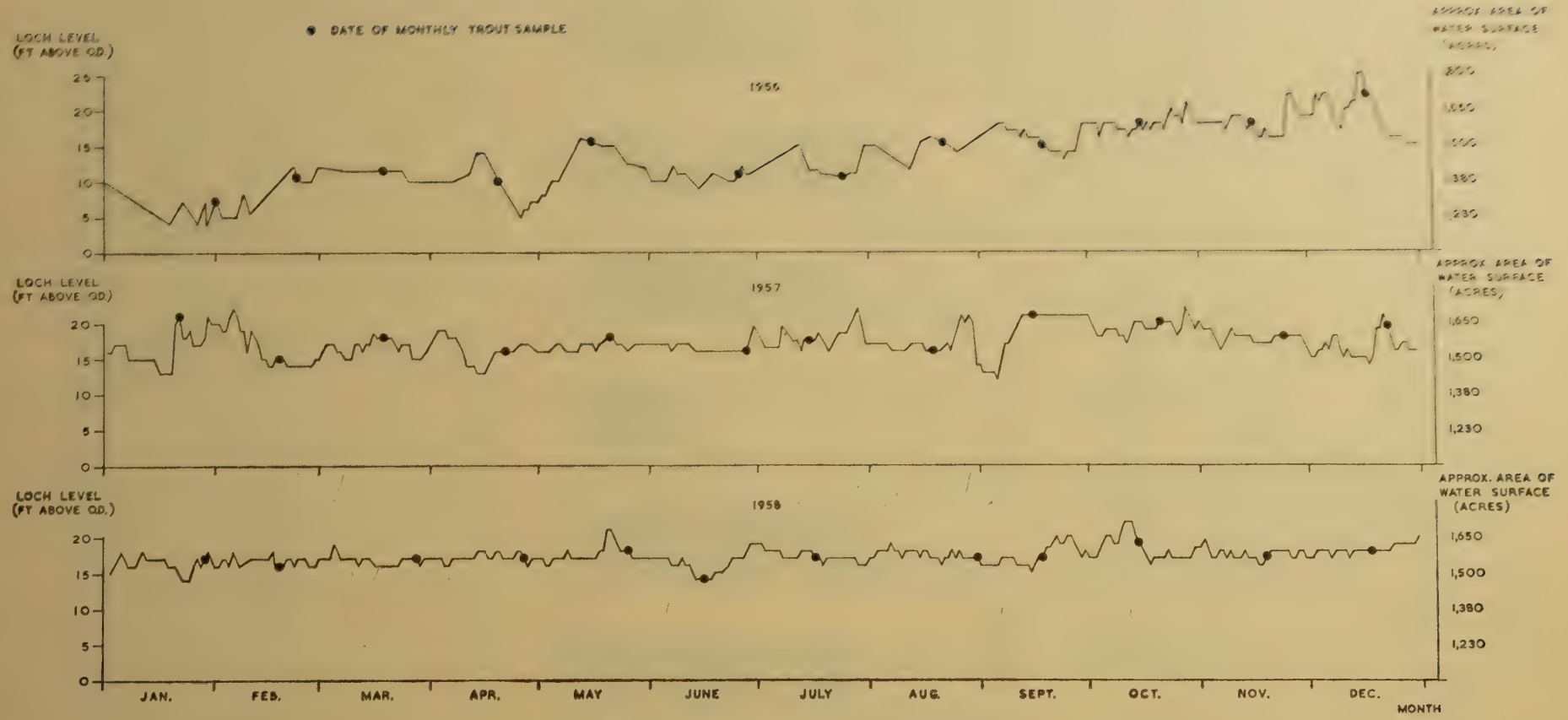


Fig. 9. Loch Garry, loch levels 1956-1958

caught in September and October 1957 and in October 1958 (Fig. 6), when, or shortly after, the loch level had risen to about 20 feet above O.D. (Fig. 9). This suggests that terrestrial fauna was now only available to trout when the loch level rose to the exceptional height of 20 feet above O.D. If this were the case terrestrial food should have become available possibly on nine occasions in 1957 and on six occasions in 1958 (Fig. 9). This situation must have occurred for short periods before impoundment whenever the loch was subject to one of its typical rises in level, but the frequency with which these fluctuations occurred is not known.

On 28th January 1958, however, a substantial amount of terrestrial food was found in trout stomachs (Fig. 6) without any corresponding rise in loch level (Fig. 9), but at that time a very sudden thaw had taken place and it is likely that many terrestrial organisms were washed directly into the loch by melting snow.

Observations on the feeding of trout in Windermere (Allen, 1938), in Loch Tummel (Campbell, 1955) and in a Swedish lake (Nilsson, 1955) indicate that they feed mostly on bottom fauna during the winter and spring and on mid-water and surface food at other times of the year. The seasonal feeding pattern of trout in Loch Garry generally agreed with that observed elsewhere (Figs. 6, 7), but it would seem that trout will feed on terrestrial organisms on the bottom at any time of the year. This seems to be true for Loch Garry and has also been observed in other impoundments in Scotland (e.g. in Loch Eigheach in June and July (Campbell, 1957) and in Loch Laggan Reservoir in April and November).

After the initial period of regular feeding on terrestrial fauna in early 1956, trout fed mostly on chironomids (larvae and pupae), wind-blown terrestrial insects and zooplankton (mostly *Daphnia* spp.) which was found in the stomachs of trout caught from June to November that year. In 1957, bottom fauna, mostly trichopteran and ephemeropteran larvae and *Pisidium* spp., formed an important part of the trout's diet from January to July, a period longer than that observed in trout from Loch Tummel but more in accordance with observations in Windermere. Chironomid larvae and pupae were important from April to September but zooplankton was only found in stomachs in April, July and August (Table 5). In 1958 a similar feeding pattern was observed with Trichoptera, Ephemeroptera and the Chironomidae again making the most important contributions.

During the three years of monthly sampling chironomids, as larvae, pupae or adults, appeared in every sample of stomachs examined, while Trichoptera appeared in thirty-four out of the thirty-six samples collected. These two groups, together with Ephemeroptera (mostly *Leptophlebia marginata* and *L. vespertina*), which were of importance from mid-winter to mid-summer, supplied the bulk of the aquatic food taken by trout in Loch Garry.

TABLE 5

OCCURRENCE OF ZOOPLANKTON IN TROUT STOMACHS

Month	Year			
	1955	1956	1957	1958
January	—	0	0	0
February	—	0	0	0
March	—	0	0	0
April	—	0	15	0
May	0	0	0	0
June	—	81	0	0
July	—	42	14	14
August	—	73	26	28
September	23	93	0	40
October	—	65	0	100
November	—	57	0	13
December	—	0	0	0

Figures show percentage of stomachs that contained zooplankton in each monthly sample.
— Indicates no sample.

The true value of zooplankton cannot be deduced from these results as there is no measure of the bulk actually ingested by trout but, from the monthly data summarised in Table 5, it appears to have been of considerable importance from mid-summer to early winter in 1956 and 1958 and perhaps also in 1957. Observations from other impoundments indicate that zooplankton flourishes during the early post-impoundment years (Runnström, 1951, Axelsson, 1961, Grimas, 1961).

C. Availability of Terrestrial Fauna as Food for Trout

Earlier work on the growth rate of trout in Loch Tummel (Campbell, 1957) has suggested that the large earthworm population of the good grazing and arable land which was flooded formed an important element in the diet of trout after flooding and played, therefore, a considerable part in the increased growth rate observed over the two years after impoundment took place. In the present investigation, therefore, a survey was made of the main types of land that were to be flooded in order to discover to what extent earthworms would be available to the trout in Loch Garry after impoundment occurred.

This survey showed that around Loch Garry earthworms were mainly limited to some small grazing fields, pockets of mineral soil, animal excrement and to the banks of feeder streams which were partly alluvial in composition. At the west end of the loch, the banks of the River Garry which were to be flooded formed two narrow strips of worm-bearing habitat about two miles long, but in the marshy land between each bank of the river and the sides of the valley, earthworms were found only in animal excrement. Small numbers of earthworms were found where the sides of the valley rose from this flat ground. The most extensive areas of worm-bearing land were some small grazing fields at Ardochy on the north side of the loch, but earthworms were also found in the thin turf that covered parts of the delta at the mouth of the Greenfield Burn.

Estimates of the density of the earthworm population in the land around Loch Garry, expressed in terms of weight, ranged from 200 lb. per acre (224 kg. per ha.) to 64 lb. per acre (71 kg. per ha.). The land around Loch Tummel was estimated to contain about 300 lb. of earthworms per acre (336 kg. per ha.). Further, the area of worm-bearing ground flooded when Loch Garry was impounded was not more than 150 acres, whereas about 700 acres were inundated when Loch Tummel was impounded. These results suggest that the quantity of earthworms available as food for trout was much greater in Loch Tummel than in Loch Garry. It is not easy, however, to assess the accuracy of this comparison. Guild (1952) points out that earthworm populations vary considerably within small areas and that it is therefore impossible to quote an average population density for worms in an area in which the habitat varies. There is also evidence from other sources that earthworms are often more available after flooding than surveys of the ground before flooding would suggest, and it also seems that a high proportion of these earthworms becomes available as a food supply for trout.

The results of the examination of the stomach contents of trout caught in Loch Garry over the first few months following flooding makes it clear that earthworms were available to trout over this period. It is known that earthworms can survive submergence for many months (Roots, 1956; Campbell, 1957) but the examination of the stomach contents of trout from Loch Garry suggests that most of the earthworms were eaten shortly after flooding and that later, further supplies, which were made available by progressive rises in loch level, were exhausted within a few days of flooding. Observations on the flooded land confirmed this indication. In mid-July 1956 earthworms were limited in their distribution to the bases of degenerating tufts of common rush (*Juncus conglomeratus* Linn.) and a few were to be found in similar situations the following September, but by November earthworms were only found in land above loch level.

At the time of year when the flooding of Loch Garry took place the surrounding land would contain, in addition to earthworms, terrestrial invertebrates in all stages of development, some in a dormant condition and therefore unable to escape being submerged. The habitat of this fauna is often wet so that its members may be able to withstand total or partial immersion for considerable periods. That this fauna provided a useful supplement to the food supplies of the trout is shown in Table 4 although no live member of the fauna was, in fact, collected from the newly flooded land round Loch Garry. Two instances were observed, however, in Loch Laggan Reservoir. In April 1959, a hand-net collection from pasture

land that had been re-flooded for more than a fortnight produced living adult terrestrial Coleoptera together with the aquatic larvae of Ephemeroptera, Trichoptera and Chironomidae. In November 1959 a similar collection was made after the same land had been re-flooded for more than a week and living spiders and corixids were collected. It was observed that in the collecting jar spiders were active under water and eventually collected on some emergent vegetation. If spiders behaved similarly under field conditions they would easily become available to trout as indeed the examination of stomach contents showed them to be (Table 4).

It was also noticed that, in nearly all the stomachs of trout that contained earthworms, a considerable amount of vegetation, mainly grass, was also found. This was quite firmly compacted and bore some resemblance to pellets cast up by birds. This was also observed in Loch Laggan Reservoir and Orchil Loch (Perthshire), and in other lochs where trout had been feeding over newly-flooded land, and suggests that trout forage among submerged terrestrial herbage and take up loose vegetation along with earthworms. This suggests further that earthworms may lie on the newly-flooded bottom and are therefore readily available to trout.

DISCUSSION

A. Changes in the Growth Rate of Trout

As anticipated, the first visible signs of the effect of impoundment on the trout was a considerable increase in their size within a few months of flooding. If the effects of impoundment had been studied only by observing the size of trout caught by anglers during the immediate years following this event it would have appeared that, from 1956 onwards, trout continued to grow faster until 1959, when a sudden decrease in their growth rate took place (Table 2). These observations would have agreed with the general opinion among anglers that the beneficial effect of impoundment on the growth rate of trout is of short duration only. Nilsson (1961) states that this occurs in many cases. In Lake Torrön in Sweden, a post-impoundment increase in the growth rate of char took place which only lasted a few years, after which a great decrease in this rate occurred (Runnström, 1951). This, however, was not the case in Loch Garry as from mid-1958 until the end of 1960 the average size of trout decreased, while during the same period the rate of growth was maintained at its higher post-impoundment level, or even continued to increase e.g. as in the older age classes (Figs. 2, 4; Table 1). This suggests that some other factor, apart from a variation in the food supply, was having an effect.

Before impoundment, Loch Garry did not attract many anglers because of the small average size of its trout but as the size improved after impoundment, anglers paid increasing attention to the loch and by mid-1957 a very great increase in their numbers was observed.

During the seasons of 1957 and 1958 large parties of anglers from considerable distances were conveyed in motor coaches to the loch where they spent the week-end fishing by all methods, including baited ground-lines, which were most effective. Similar situations have arisen following the formation of impoundments elsewhere. For example, Eschmeyer (1942) records an increase in angling intensity following the impoundment of rivers in the Tennessee Valley and, in Scotland, the sequence was similar after the impoundment of Loch Tummel in 1950 and of Loch Eigheach in 1953. An increase in angling is likely to occur in most parts of Scotland whenever it becomes widely known that exceptionally good angling is available on a large scale and many anglers probably know that such conditions exist in newly-impounded reservoirs.

From mid-1958 onwards, large fluctuations occurred in the average size of the trout sampled, but by this time the pressure of angling was an important factor, and it is likely that some of these samples may have been collected during, or just after, periods of great angling activity. This would produce a local scarcity of the larger trout to begin with and, ultimately, a general scarcity. It is possible that after three years of considerable angling effort an actual decline in the number of larger trout had taken place. As no estimate of the numbers of trout caught could be made regular sampling was discontinued after December 1958.

As well as the reduction in the numbers of trout due to the amount of angling, the recruitment of young trout into the loch might have also been affected by the rising loch level.

Runnström (1952) in Sweden and Sømme (1958) in Norway found that the spawning grounds in streams entering lakes were inundated by a rise in lake level following impoundment and this may also have affected the trout population of Loch Garry where, as in many Scottish lochs, the lower reaches of the feeder burns are the most important spawning grounds because the gradient of the middle and upper reaches of these burns is too steep. Some of the effects of the relationship between spawning facilities, population density and rate of growth of trout have been discussed by Campbell (1960).

The combined effects of a reduction in population density and a possible increase in the numbers of aquatic organisms may have been responsible for the continuation of the improved rate of growth in 1957 and 1958.

Intensive cropping of a trout population can affect the growth rate of trout and their size distribution (Dahl, 1919). Reduction in the numbers of trout in Loch Garry would tend to increase their rate of growth and this would make the effect of the lack of terrestrial food and any possible decline in the numbers of the bottom fauna, after an initial post-impoundment increase, less noticeable. It was apparent, therefore, that after 1957 (although this was not obvious until much later) the natural course of events following impoundment affecting a population of loch trout could not be observed in Loch Garry and the subsequent pattern of growth of these trout was the result of a complex situation.

Dahl (1919) observed that when the numbers of trout in two Norwegian tarns were reduced by netting an increase in the growth rate and numbers of young trout took place, while the numbers of larger and older trout decreased and concluded that the growth rate of trout is increased by a reduction in their numbers. These observations offer an explanation why, in Loch Garry, trout in their second year did not show an increase in rate of growth until 1958 onwards. They also suggest that immediate post-impoundment conditions, with an abundance of terrestrial food available are not so favourable for the growth of smaller trout as a reduction in the population followed by a relative increase, perhaps even an actual increase, in the amount of aquatic food. The large average size of terrestrial organisms compared with the average size of aquatic organisms might also be an important factor influencing the growth of the smaller trout. The increase in the rate of growth of trout in their first year, from 1957 onwards (Table 1 and Fig. 2) suggests that these small trout were also subject to similar effects, particularly in the Greenfield Burn estuary where a proportion may have experienced loch conditions during their first year of life. These conditions may have been particularly favourable for growth as Grimas (1961) found that in a regulated lake a greater abundance of bottom fauna occurred in the vicinity of inflowing burns.

B. The Effect of Terrestrial Food on the Growth of Trout

Data on the rate of growth of trout in Loch Garry and in other newly-impounded waters (Frost, 1956; Campbell, 1957, and others) suggest that the amount of food available to trout when a terrestrial habitat is first flooded is much greater than that normally available in an aquatic environment and, as a loch increases in volume the population density of the trout is temporarily reduced so that the feeding area per trout is increased. A further factor is that, in an established loch, the amount of food available to trout over a short period is only a small proportion of the bottom fauna but in a flooded terrestrial habitat it is probable that a large proportion of the standing crop of invertebrate fauna becomes immediately available as individual organisms attempt to escape from, or are incapacitated by, the rising water.

Quantitative estimates of the standing crop of the bottom fauna in Scottish lochs are very few. It was estimated, however, that the standing crop of the bottom fauna of the littoral zone of two Highland lochs, with physical and chemical characteristics similar to those of Loch Garry, was 25 and 36 lb. per acre (28 and 40 kg. per hectare) respectively. Estimates for the fauna of the bottom mud of four lochs were 4, 5, 19 and 58 lb. per acre (4·5, 5·6, 21·0 and 65·0 kg. per hectare). In the flooded land around Loch Garry the standing crop of earthworms alone would have been as great or greater.

The rate of growth of trout in Loch Garry may also have been increased because the weight of individual terrestrial organisms taken by trout was four to five times that of the aquatic organisms. A trout could,

therefore ingest a large bulk of food with a relatively small output of energy; this has been discussed by Stube (1958). For instance, the average weight of the stomach contents of twenty-six trout caught in February 1956 (5 g.) could have been made up of only seven to ten earthworms, whereas approximately 600, 12 mm. chironomid larvae; 115, 10 mm. ephemerid nymphs or 40, 15 mm. limnophilid larvae would have had to be eaten to produce the same weight of stomach contents. It was observed, however, from the analyses of 663 trout stomachs containing food, that aquatic organisms were seldom taken in these amounts, e.g. the greatest number of chironomid larvae found in any trout was 258 and only four other trout contained over 100 of these larvae; the greatest number of ephemerid nymphs was 173 and only two other trout contained over 100, and 40 trichopteran larvae were the most found in any trout, while only six trout contained over 20, most of which were less than 15 mm. in length. Where stomachs contained an assortment of aquatic organisms, the greatest number of individuals was 228. These observations on trout from Loch Garry may be compared with similar ones made on trout from Loch Tummel where, although the average weight of the trout sampled was about four times that of the trout sampled from Loch Garry, the greatest number of aquatic organisms found in any stomach was 335 (306 nymphs of *Leptophlebia marginata*, and 22 pupal chironomids) and only eight other trout, out of 121 sampled, contained more than 100 organisms. The trout examined from both lochs were taken at all seasons and included fish caught at all times during the day and night.

The food value of insect larvae and earthworms also differs as Geng (1925) has shown that chironomid larvae are composed of about twice as much and ephemerid larvae about four times as much indigestible chitinous material as earthworms and he adds that the protein value of natural fish foods increases with the size of the organisms. As well as the larger average size of terrestrial organisms and consequently the greater food value obtained from them a further possible benefit to trout feeding over newly flooded land is that they may actually ingest a greater bulk of food, when the individual organism is large, than when feeding on aquatic organisms, which in this case are much smaller.

The rate of passage of food through the alimentary canal may also be important as, if certain organisms tend to accumulate in the stomach while others pass through rapidly, a false idea would be obtained of the numbers of organisms eaten. In a laboratory experiment it was found that earthworms and *Gammarus* (representing an aquatic organism) fed separately to small trout (9-17 cm. in length) passed through their stomachs in about 55 hours at water temperatures which ranged from 4·5-4·9°C; a range which corresponds with the early spring water temperatures in Loch Garry.

To sum up, some possible reasons for the increase in the growth rate of trout feeding over the newly-flooded land around Loch Garry are (a) the increase in the amount of food organisms available (b) the larger average size of terrestrial organisms which resulted in trout obtaining more food with less effort and (c) the possibility that trout actually ingested a greater bulk of food as the terrestrial food organisms were larger.

C. The Effect of Impoundment on the Aquatic Food of Trout

As no quantitative studies of the density of the invertebrate fauna were carried out during this investigation there is no direct evidence of an increase in the numbers of these organisms following impoundment. The pre-impoundment survey by Hamilton (personal communication) suggested that the reduction in the level of the loch, together with its natural fluctuations, reduced the littoral fauna. Post-impoundment conditions may have been more favourable, because Ephemeroptera and Trichoptera were well represented in trout stomachs in 1957 and 1958 (Table 6), whereas both these groups of insects were considered scarce by Hamilton and in 1957 and 1958 mass emergences of the ephemerid *Leptophlebia marginata* were observed over flooded land during April and May. The continued, increased rate of growth of trout in Loch Garry also suggests that an increase did, in fact, occur. Terrestrial food organisms were probably available at intervals until December 1956, when the loch level reached its present maximum, but from then onwards they were probably only available in exceptional circumstances such as occurred in September and October 1957 and in January and October 1958. The increased rate of growth of trout in Loch Garry must have been maintained, therefore, by an increase in the amount of aquatic organisms, as suggested by Table 6, at least until 1958, when the effect of a possible reduction in population density may have begun to be important.

TABLE 6

THE NUMBER OF AQUATIC ORGANISMS IN THE STOMACHS OF TROUT SAMPLED IN MAY AND SEPTEMBER 1955 (PRE-IMPOUNDMENT), 1956, 1957 AND 1958 (POST-IMPOUNDMENT)

a) May Samples

Organism	No. per Sample			
	Year			
	1955	1956	1957	1958
Gordiacea	1	0	0	0
Insecta				
Plecoptera, larvae	0	1	1	0
Ephemeroptera, all stages	2	28	489	100
Odonata, larvae	1	0	0	0
Hemiptera				
Corixidae	0	0	0	1
Neuroptera, Sialis larvae	0	1	0	1
Trichoptera, all stages	1	17	44	21
Coleoptera, larvae	0	0	2	0
Diptera				
Chironomidae, all stages	0	10	1154	1833
Mollusca				
Gasteropoda				
Limnaea pereger	27	0	0	1
Lamellibranchiata				
Pisidium spp.	0	0	0	2
	32	57	1690	1959
No. of stomachs examined	14	21	18	14
Av. No. of organisms/stomach	2·3	2·7	94	140

b) September Samples

Organism	No. per Sample			
	Year			
	1955	1956	1957	1958
Insecta				
Plecoptera, larvae	3	1	0	0
Trichoptera, all stages	4	6	3	41
Coleoptera, all stages	0	0	2	0
Diptera				
Chironomidae, all stages	20	371	726	80
Arachnida				
Hydracarina	0	0	0	1
Mollusca				
Gasteropoda				
Limnaea pereger	43	0	0	0
	70	378	731	122
No. of stomachs examined	13	14	7	5
Av. No. of organisms/stomach	5·4	27	104	24·4

Zooplankton was also present in three of the stomachs examined in 1955, in thirteen in 1956 and in two of the stomachs examined in 1958.

Large numbers of certain aquatic organisms have been recorded in other bodies of water which have been newly impounded. Axelsson (1961) states that the submergence of terrestrial areas improves environmental conditions for zooplankton. In Scotland, when Loch Crannoch, an artificial body of water made by the impoundment of a small stream, was re-flooded after being empty for four years, small chironomid larvae were very numerous in shallow water after only one month; 100 ml. of water contained 894 of these organisms. A month later, a considerable increase in the numbers of planktonic Crustacea was observed, and in less than one year *Gammarus pulex* was present all round the loch in considerable numbers (Morgan, personal communication). In Ladybower Reservoir, Derbyshire, *Daphnia* spp. and *Bosmina* spp. became abundant just over four months after impoundment. The following year *Daphnia* spp. were again plentiful (while chironomid larvae were also present in considerable numbers) and young trout introduced into the reservoir grew rapidly (Thompson, 1946). The impoundment of Eyebrook Reservoir began in January 1940 and *Daphnia* spp. were observed during the first spring after flooding. Trout introduced into this reservoir grew exceptionally rapidly (Oliver, 1948).

Nursall (1952) records that after the impoundment of Barrier Reservoir in Alberta, in May 1947, plankton and chironomid populations became rapidly established during the summer and that the peak weight of the standing crop of post-impoundment bottom fauna occurred during the first winter, and was largely composed of larval Chironomidae. In some Norwegian and Swedish reservoirs fish benefited from an increase in Cladocera, particularly *Daphnia* spp. and *Eurycercus lamellatus*, as a result of impoundment (Aass, 1958; Runnström, 1951).

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The aerial photographs of Loch Garry are reproduced by permission of the Air Ministry.

SUMMARY

1. Loch Garry, in Inverness-shire, became a hydro-electric power reservoir during the winter of 1955-56. The food, feeding habits and growth of its brown trout, as well as major environmental changes in their habitat, were studied just before and during the three years following this event.
2. Trout that were in their third, fourth, fifth and sixth years when flooding took place, showed a considerable increase in their rate of growth during 1956. After 1956 this faster rate was maintained by trout during their third year, while for trout in their fourth, fifth and sixth years the growth rate continued to increase further.
3. Trout in their first and second years did not show any immediate response to early post-impoundment conditions.
4. In general terms, before impoundment, only 10% of the trout in Loch Garry were of a size that could be considered worth retaining by anglers. This proportion rose to over 50% in 1956 and to 80% in 1957.

5. The first indication of a post-impoundment change in growth rate was contained in the sample of trout collected in mid-March 1956.
6. In the first five monthly samples after flooding, terrestrial food predominated in the stomach contents of trout. The ratio of terrestrial to aquatic organisms found in trout stomachs was 19:1 by weight and 4·3:1 by numbers.
7. Of the terrestrial organisms found in trout stomachs during the early months of 1956, earthworms predominated both numerically and in bulk. Spiders were the next most numerous organisms, but provided less bulk than coleopteran, lepidopteran and dipteran larvae. Trout fed on terrestrial organisms on the bottom at all times of year.
8. The increase in the average size of trout in Loch Garry, following impoundment, resulted in a great increase in angling pressure which was considered likely to have had repercussions on the population density and rate of growth of the fish.
9. Some possible reasons for the increase in the growth rate of trout soon after impoundment are (a) an increase in the amount of food available, (b) the larger average size of terrestrial food organisms which results in trout obtaining more food with less effort and (c) that trout actually ingest more when the units of food are larger.
10. The increase in the numbers of aquatic organisms found in trout stomachs after impoundment suggest that an increase in the bottom fauna may have taken place.
11. As a result of impoundment there is now a greater area of shallow water in Loch Garry than before. This should have a beneficial effect on trout production.

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APPENDICES

A. Factors Affecting Future Trout Production in Loch Garry

The sequence of events that probably takes place in new impoundments can be summarised as:

(a) On impoundment, terrestrial organisms become available to fish as food.

(b) Within a short time after impoundment increases take place in the numbers of Cladocera and Chironomidae.

(c) A general increase in the numbers of the bottom fauna takes place.

These events result in a great increase in the growth rate of the fish. However, the future fish production of an impoundment appears to depend mostly on its physical characteristics and is difficult to predict. Rawson (1955) emphasises that it is most difficult to make predictions of productivity in newly-made reservoirs or lakes with disturbed levels because present knowledge and methods only allow crude estimates to be made. If the physical characteristics of a new reservoir are known, it should be possible, by comparison with natural lakes in the same region, to predict the major physical and biological features.

The physical features of reservoirs vary widely. For instance, Eyebrook Reservoir in Northamptonshire, has a maximum depth of only 35 feet and when the sides become exposed during a dry summer they are colonised by a 'luxurious' crop of terrestrial vegetation, which in turn is presumably colonised by terrestrial invertebrates. When the water level rises and the vegetation rots, great biological activity ensues (Oliver, 1948). A similar situation arose after a succession of dry years in Norris Reservoir in the Tennessee Valley (Wood and Pfitzer, 1958). The other extreme in productivity is described by Aass (1958) and Nilsson (1961), in some impoundments in Norway and Sweden. These are subject to large fluctuations of level which produce a wide, impoverished erosion zone and much of the shallow water bottom fauna, which provided the bulk of the food of trout, is greatly reduced in number as it cannot withstand long periods of freezing or desiccation. In Lake Blåsjön, in Sweden, this fauna was reduced by 70% after regulation (Grimas, 1961). A similar type of reservoir, Lake Minnewanka in Alberta, is described by Cuerrier (1954) and Rawson (1955). Here fluctuations of water level resulted in a 50% decrease in the weight of bottom fauna in the first three years after impoundment. The bottom fauna then increased and after 10 years was 75% of the original weight although greatly changed in composition, as chironomid larvae, which originally constituted 52% of the bottom fauna, now constituted 93%, while larger organisms of the littoral fauna which were important as trout food, were greatly reduced. These reservoirs did not suit trout as the latter rely to a considerable extent on shallow water fauna. Similarly, the impoundment of Lake Borgasjön in Sweden resulted in changes in the composition of the bottom fauna with the reduction or partial disappearance of several forms, chironomids again becoming more important than before as trout food (Stube, 1958). In Scotland, Loch Laggan Reservoir and Loch Treig Reservoir, both in Inverness-shire, are examples of this type, while several other new hydro-electric reservoirs are developing along these lines.

From these observations it appears that the chief physical characteristic that affects the production of trout food in a reservoir is the extent and duration of variations in level and the nature of the littoral zone. Nilsson (1961) compares two Swedish reservoirs, one with a considerably greater drawdown than the other. In the former the numbers of trout food organisms were greatly reduced while in the latter these organisms were far less affected. Parsons (1958) compares fish production in storage reservoirs and mainstream reservoirs in the south east United States. The storage reservoirs were subject to large fluctuations of level while mainstream reservoirs had a much more stable water level and produced more fish.

Loch Garry is the headpond of a two-stage cascade arrangement, with Loch Quoich, further up the river system, as the storage reservoir; it also receives some water from feeder streams. The power station

at Invergarry generates on a narrow range of heads, normally about two to three feet, so that the water level of the loch does not vary greatly although it may at times rise rapidly as it has always done (Fig. 9). As a result, a wide erosion zone has not been formed. Furthermore, in Loch Garry most of the flooding took place over level or gently sloping land in the river valley at the west end of the loch, so that even when the loch level is abnormally low by present standards, a considerable area of shallow water remains, with the result that the shallow water bottom fauna is comparatively safe from freezing or desiccation. This situation is in contrast with that described by Scandinavian and North American workers. In these countries hydro-electric reservoirs are at their maximum level during the summer and at their minimum level by the end of winter. In Scotland the reverse is generally true, although periods of high or low level can occur at any time of year.

Another aspect of the physical effect of impoundment on the fish population is the effect on the rate of growth of fish resulting from the loss of spawning facilities. Aass (1958) states that a lasting improvement in growth rate may result from a loss of spawning grounds as the reduction of the fish population can compensate for the decrease in fish food production.

Reviewing the situation in Loch Garry in the light of these observations it is likely that, considering the adverse pre-impoundment conditions mentioned by Hamilton (personal communication) and that now more shallow water exists than before, the production of trout food in the loch may have actually been increased as a result of impoundment. Trout production in the future may depend, therefore, on the rate of recruitment of young fish to the loch. If spawning facilities have in fact been reduced trout will continue to grow at an improved rate. If, on the other hand, these facilities have not been reduced the loch will again become overstocked, and the growth rate will decrease, possibly to its pre-impoundment level.

B. Post-impoundment Shore Line Development

Terrestrial vegetation did not degenerate quickly after impoundment but where the sides of the loch were steep, and therefore exposed to strong wave action, the vegetation mat was soon broken up and underlying rocks and boulders exposed.

Grass in the littoral zone was still alive, though covered with algae, after five month's submergence. Along the less exposed parts of the new shoreline much of the original vegetation was still intact in July 1957 but an intermediate zone between the permanently submerged bottom and the normal terrestrial habitat (the beach zone of established lochs) was becoming more defined. A year later, in July 1958, some thirty months after impoundment, the permanent bottom was bare peat or soil, bearing tufts of dead vegetation. The intermediate zone was devoid of a vegetation mat and also of dead herbage, which had presumably been broken up by wave action, but supported occasional bushes of sallow (*Salix caprea* Linn.) and bog-myrtle (*Myrica gale* Linn.) which had survived, along with the stumps of felled trees. The zone had also been colonised to some extent by a sedge (*Carex* spp.), toad-rush (*Juncus bufonius* Linn.) and at least two mosses (*Scorpidium scorpioides* (Hedw.) Limpr.) and *Sphagnum* spp.).

Where the sides of the loch sloped gently the rate of erosion was slow, in contrast to the rapid rate where the sides were steep and wave action had much more effect. Other factors which have affected the rate of erosion were the long period of survival of the terrestrial herbage mat and the colonisation of the erosion zone by some new species of vegetation and, more than five years after impoundment, roots and root fibres of dead vegetation (trees, heather, bracken and grass) still had a stabilising effect on the top soil and peat. The daily fluctuations of loch level caused by generation requirements (Fig. 9) superimposed on large natural fluctuations have, in these areas, tended to reduce wave action, as this is not concentrated along one level of the shoreline for any length of time.

The survival of terrestrial herbage subjected to flooding can be observed in several other reservoirs. In Loch Laggan Reservoir, which has been impounded for over 25 years, an area of rough pasture is flooded whenever the reservoir fills to capacity. In the five and a half years from September 1954 to February 1960 this grass land has been flooded for over five months at a time on three occasions, and altogether it has been under water for 36% of the whole period. The herbage consists mostly of tufted hair grass (*Deschampsia caespitosa* (L.) Beauv.) and creeping bent (*Agrostis stolonifera* Linn.).

The possible future development of the shoreline of Loch Garry is suggested by comparison with Loch Tummel, a reservoir with similar fluctuations in level, which has now been impounded for ten years. Around this loch, where the shoreline is steep, beaches have been formed, backed by earth cliffs which are still subject to erosion by strong wave action. Where the sides of the loch slope gently two types of development have occurred, (a) where the shoreline is exposed, a shingle beach has been formed, backed by a strip of common rush (*Juncus conglomeratus* Linn.) above the high water level mark or (b) in sheltered areas, the original soil is still intact and below the strip of typical common rush plants is an area of stunted common rush, which exist in the zone affected by the regular fluctuations in loch level. The trunks and roots of trees are still firmly embedded in the littoral zone and, with the other dead plant remains, which are permanently submerged, are likely to exist for a very long period. In some Norwegian reservoirs tree trunks are exposed when the level drops, even after nearly forty years (Aass, 1958). In small Highland reservoirs heather tufts and other plant remains have been found *in situ* after half a century of submergence as plant decomposition is not a rapid process in these acid waters.

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